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Different cation stresses affect specifically osmotic root hydraulic conductance, involving aquaporins, ATPase and xylem loading of ions in *Capsicum annuum*, L. plants

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Summary

In order to study the effect of nutrient stress on water uptake in pepper plants (*Capsicum annuum* L.), the excess or deficiency of the main cations involved in plant nutrition (K^+, Mg^{2+}, Ca^{2+}) and two different degrees of salinity were related to the activity of plasma membrane H^+-ATPase, the pH of the xylem sap, nutrient flux into the xylem (J_s) and to a number of parameters related to water relations, such as root hydraulic conductance (L_0), stomatal conductance (g_s) and aquaporin activity. Excess of K^+, Ca^+ and NaCl produced a toxic effect on L_0 while Mg^{2+} starvation produced a positive effect, which was in agreement with aquaporin functionality, but not with ATPase activity. The xylem pH was altered only by Ca treatments. The results obtained with each treatment could suggest that detection of the quality of the nutrient supply being received by roots can be related to aquaporins functionality, but also that each cation stress triggers specific responses that have to be assessed individually.

Introduction

An excess or absence of the main elements in plant nutrition can cause disorders with respect to nutrient availability, uptake, transport or partitioning within the plant. In addition, solubility and competition factors may result in deficiencies of

Abbreviations: L_0: hidraulic conductance; g_s: stomatal conductance; J_s: flow of solutes into the xylem

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other nutrients, as well as a variety of physiological disorders (for example, related to water balance). Some of the parameters of water relations that can be affected include the hydraulic conductance of roots, stomatal conductance in the leaves, and, at the cellular level, the activity of aquaporins (Clarkson et al., 2000).

In plants, water transport across tissues is a fundamental process that must be adapted sufficiently to different environmental conditions in order to allow plants to survive. Similarly, nutrient uptake is a related function which, in most cases, depends on water movement. Under conditions of high transpiration, water moves passively across the roots at a high rate, whereas, under high humidity and in the absence of transpiration, the ascending water flow to the shoot is generated by root pressure with low flow rates (Steudle, 2000). Aquaporins, membrane channel proteins that facilitate and regulate the permeation of water across biological membranes (Baiges et al., 2002), have been found in the plasma membrane and tonoplast. Aquaporins make different contributions to water transport, depending on the environmental conditions. They are part of the mechanism of the transcellular pathway (Steudle, 2000), together with simple diffusion across the plasma membrane (Carvajal et al., 1998). In this way, water flow may be regulated by the opening and closing of aquaporins, which have been shown to be affected by various environmental factors, such as salinity (Cabañero et al., 2004), nutrient deprivation (Carvajal et al., 1996) and drought (North and Nobel, 2000). The molecular and cellular mechanisms that link hormonal, nutrient or stress stimuli to the activity of aquaporins in root cell membranes remain poorly understood.

The plasma membrane H^+-ATPase plays an essential role in the maintenance of plant cell turgor and extracellular pH. Using energy released by hydrolysis of ATP, the H^+-ATPase exports protons to create an electrochemical gradient across the plasma membrane, which is then used by the cell as the driving force for ion and metabolite transport. Regulation of this enzyme may play an important role in the response of plants to different stressing environments, in order to maintain control of ion transport. Also, previous studies have shown that aquaporins can be gated by protons (Gerbeau et al., 2002), indicating that H^+-ATPases may have an important role in water transport across plant membranes (Luu and Maurel, 2005).

The pH of the xylem sap is very relevant for loading/unloading processes, as it constitutes the driving force for antiport and symport activities and is the regulator of ion transporters or signalling molecules. Measurements on xylem sap collected from root exudates have shown a slightly acidic pH in the range of 5.5–6.5 (López-Millán et al., 2000). The xylem appears to exhibit a high capacity to maintain pH at a set value (Senden et al., 1992). However, in response to stress conditions, the xylem pH can fluctuate (Wilkinson and Davies, 1997), likely due to alterations in the H^+-ATPase or H^+-exchange systems in the plasma membrane of vessel-associated cells.

Potassium, calcium and magnesium are essential macronutrients and are normally the most abundant cations in plants. Potassium is essential for many metabolic processes and is a major contributor to cell turgor, whereas calcium plays a number of roles in stabilising cell walls and membranes and as a secondary messenger. Magnesium acts as a bridging element, forming complexes of different stabilities, which confers upon it a high capacity to interact with strongly nucleophilic ligands. In contrast, Na^+ is normally a non-essential element that is toxic to many plant species when present in high concentrations. Physiological interactions between these cations are well-documented (Carvajal et al., 2000a, b).

Often, an excess of certain nutrients in the external solution can be overcome by a controlled xylem-loading system, where the nutrients are introduced into the xylem stream and delivered to the whole plant. Since the fluxes and loading of Mg^{2+} and Ca^{2+} appear to be strongly related with the water stream, aquaporins and divalent-cation channels can mediate these processes. Sodium entry into the root symplast is most likely mediated by weakly-voltage-dependent, non-selective cation channels (Demidchik and Tester, 2002). Potassium loading into the root xylem may be a pH-sensitive process, the pH modulating the activity of K^+ channels responsible for loading K^+ into the xylem (Lacombe et al., 2000). Whereas the K^+ channel responsible for K^+ uptake into the root symplast is AKT1, xylem-loading of K^+ is regulated separately from K^+ uptake from the external solution (Engels and Marschner, 1992).

The aim of the present work was to examine the effects of an excess or deficiency of the main cations in plant nutrition (K^+, Mg^{2+}, Ca^{2+}), and of two different degrees of salinity with the water relations and xylem ion loading in pepper plants. Our hypothesis was that nutrient uptake disorders might influence plasma membrane H^+-ATPase activity, a parameter that is related closely to pH, nutrient flux into the xylem and to diverse parameters of water relations such as root hydraulic conductance, stomatal conductance and aquaporin activity.